

SOME OBSERVATIONS ON THE BEHAVIOUR OF FEMALES OF *PHILANTHUS TRIANGULUM* (F.) (HYMENOPTERA, SPHECIDAE)¹⁾

by

R. T. SIMON THOMAS & A. M. J. SIMON THOMAS

Pharmacological Laboratory of the University of Amsterdam

In connection with research on the mechanism of action and the chemical structure of paralysing wasp venoms, females of *Philanthus triangulum* (F.) (Sphecidae, Hym.) have been collected in the southwestern part of France since 1965. Since these animals can only be caught during the summer, attempts have been made to breed them in the laboratory (Simon Thomas 1966), but failure to bring about mating under laboratory conditions has made continuous breeding impossible. In the search for a better breeding method, the behaviour of *P. triangulum* in the field was investigated.

Ordinarily, *Philanthus triangulum* preys on honey bees and, according to Beekhuis van Till (1935), occasionally on solitary bees (*Andrena*, *Dasygaster*, *Megachile*, and *Halictus*). The females of *P. triangulum* feed on some of the paralysed bees, sometimes by pressing the honey from the bee's stomach by means of rhythmic abdominal movements, sometimes by biting the prey just behind the first pair of legs and sucking the haemolymph (Hirschfelder 1952). The majority of the captured, paralysed bees is used for food for the larvae.

The behaviour of *Philanthus triangulum* has been described by Tinbergen (1932) and van Beusekom (1946), who investigated orientation, and by Beekhuis van Till (1935), who gave a detailed description of the reproductive behaviour. Other data have been collected by Bouwman (1927), Bouvier (1916), Picard (1903), Roth (1917), and Vergne (1935). However, these studies do not provide a complete picture of the behaviour of this insect and we therefore undertook further research between 1968 and 1970. Since *P. triangulum* had disappeared from The Netherlands in 1960, the observations were made in southwestern France near Linxe (Department of Landes) in an almost flat, sandy area, an excellent biotope for this wasp. In 1968 a colony near Linxe was studied and in 1969 and 1970 another colony near Naboude (Fig. 1). Most of the observations were made in 1969 on the colony near Naboude, situated on a sandy cart track running more or less East-West. The nests were located between the ruts in the untravelled middle part of this track, and also on both verges. The colony received sunlight throughout most of the day. On both sides of the track, there was a stand of pines (*Pinus pinaster* Ait.), about 5 m high, with a ground cover of heather (*Erica cinerea* L.) and furze (*Ulex nanus* Forst. and *U. europaeus* R.).

¹⁾ Supported in part by the European Research Office, United States Army, London, United Kingdom of Great Britain.

METHODS

During the observation periods, the temperature and humidity were registered with a thermo-hygrograph mounted 2 m above the ground. Unfortunately, these measurements had to be made at a distance of 8 km from the research area. Data obtained from the meteorological stations of Cazaux and Mont-de-Marsan were also taken into account. The heat content (the sum of the air temperatures in degrees Centigrade above 25°, added per hour between 10 a.m. and 6 p.m.) was calculated for all the observation days. On the basis of the heat content the days were classified as hot (heat content > 50), moderately hot (heat content between 50 and 0), and cold days (heat content 0, i.e. maximum temperature < 25° C).

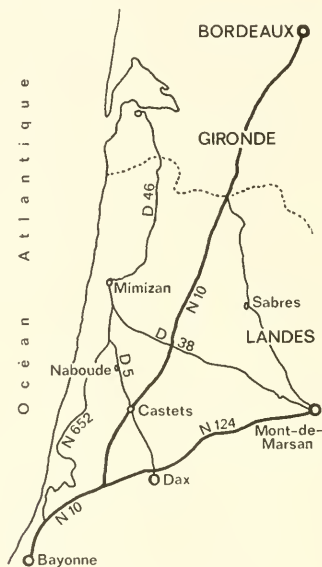


Fig. 1. Location of the study area, near Naboude in southwestern France

For the study of the behaviour of individual wasps, the thorax was marked (Simon Thomas 1970). If two lines were used, the colour of the left line is mentioned first; if the marking consisted of a dot in a circle, the notation sequence is as follows, C (circle), colour of the circle, colour of the dot (e.g. CYR). Nests of individual females were marked with one or more coloured marking pins.

Casts were made of six nests, by filling them with prevulcanized latex, a product which can be mixed with water in any given proportion to obtain the desired viscosity. After the material had hardened the casts were dug out carefully.

In 1969 the observations were made continuously from July 7—28 and from August

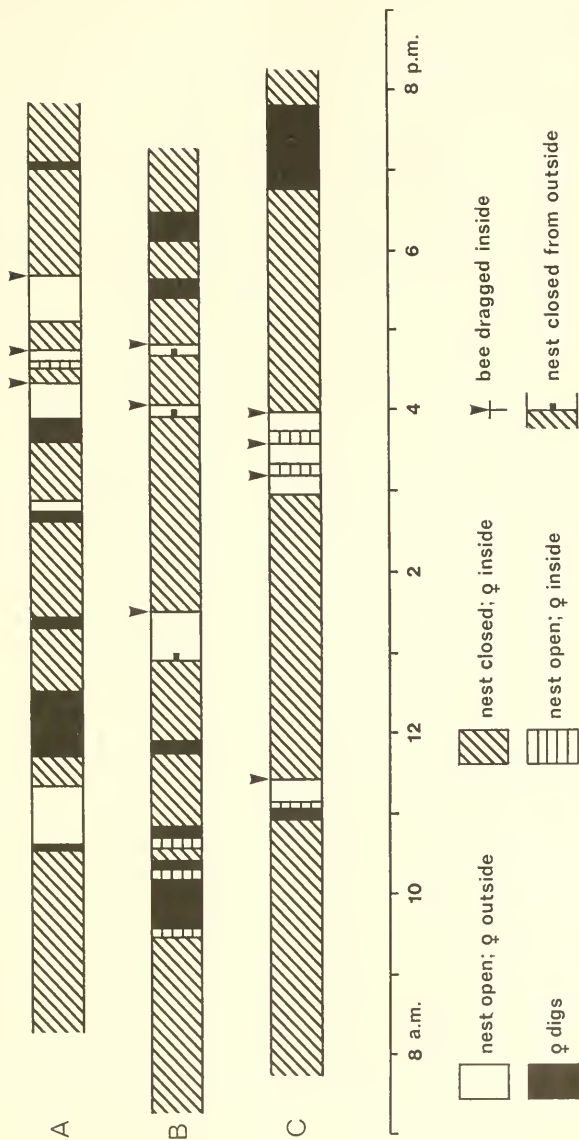
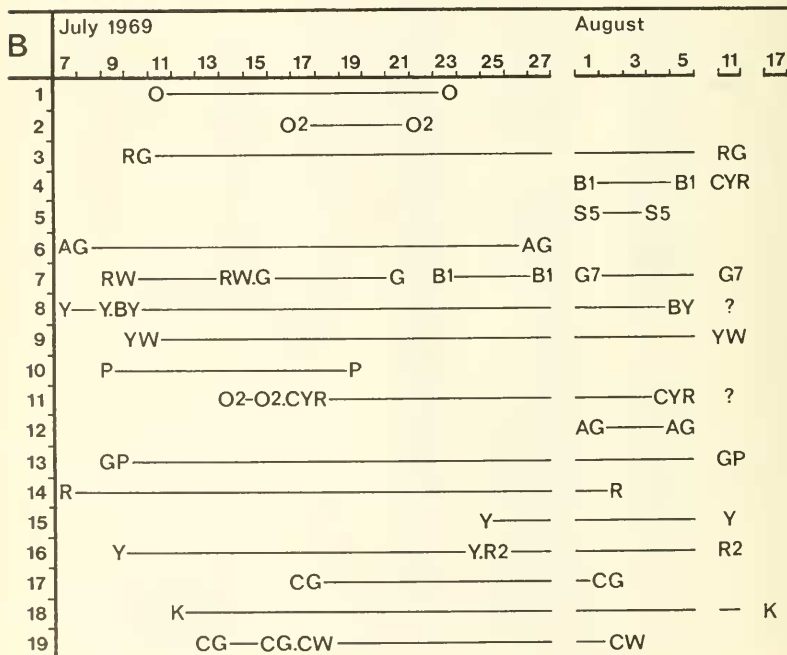
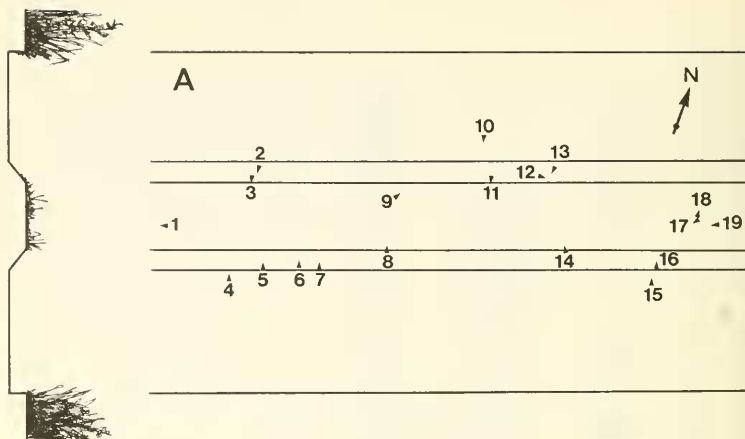


Fig. 2. Diagram of representative behaviour of three females on a moderately hot day; A, female digging a new nest; B, female closing its nest from the outside; C, female bringing home a single bee and a series of three bees



1—5, as well as on August 11, starting in the morning before the first females opened their nests until the evening, after all the nests had been closed for the night. In 1970 the observations were made continuously from June 17th through July 17th. To find out whether the nests were opened during the night, white sand was strewn on the outer closure.

The research mainly concerned the behaviour of females; males were observed only when they returned to their sleeping holes, in the evening or at the approach of a shower.

RESULTS

Table 1 shows the climatological data for the periods of observation in 1969 and 1970, including the heat content and the incidence of rain. No data on climate conditions are available for 1968.

In 1968 the first male was seen on June 12th and the first female on June 19th. For 1969, these dates were June 22nd and 24th and for 1970, June 19th and 29th, respectively.

General description of the behaviour on a moderately hot day

The females spend the night in their own nests, which are kept closed (Fig. 2). In the morning the nest is opened. The female emerges, usually starts digging the sand away from the entrance, and then flies off, either to suck nectar or to capture a bee. All day long, paralysed bees are carried into the nests. At the end of the day the female digs for a long time and removes the sand lying in front of the entrance. Finally, the nest is closed with a plug of sand pushed outwards. Fig. 3 shows the location of the nests at the observation site, the duration of the periods during which the nests were occupied, and the colour code of the female then living in a particular nest (1969). It is evident from Fig. 3 that many females occupied the same nest for a long period of time.

Every form of activity proved to be influenced by temperature. Rain strongly reduces any activity. On rainy days no bees are caught.

Detailed description of a number of behaviour patterns

a. Awakening.

Under awaking is understood the first perceptible activity of the female of *Philanthus triangulum*, which consists of removing the outer plug of sand from the entrance of the nest. After the opening of the nest, the female's head appears in the entrance and after some time the female emerges. In cold weather it stays in the entrance for a long time

Table 1. Climatological data in Naboude (France) during the observation periods of 1969 and 1970; heat content is the sum of the air temperatures in degrees Centigrade above 25, added per hour between 10 a.m. and 6 p.m.

	Heat content	1969	1970
Number of observation days		24	31
Number of hot days	> 50	3 (12.5 %)	2 (6 %)
Number of moderately hot days	< 50, > 0	15 (62.5 %)	12 (39 %)
Number of cold days	< 0	6 (25 %)	17 (55 %)
Number of rainy days		3 (12.5 %)	9 (27 %)

Fig. 3. A. Location of the 19 nests between the ruts in a cart-track near Naboude. At the left, a cross-section of the track. Arrows point in the direction of the burrow. B. Periods during which the females occupied the 19 nests

after having removed the outer plug. The time of awakening varies from specimen to specimen and per specimen, from day to day. Although no clear relationship with temperature was demonstrable, the impression was gained that the appearance is delayed after a cold night. Also, the animals appear to awake earlier on hot days than on cold days.

b. Digging.

The nest dug by *Philanthus triangulum* can be recognized by the shape of the mound (the cone of sand situated in front of the entrance). This mound roughly resembles that of *Dasydoda hirtipes* L. (Apidae, Hym.), although in the case of the latter the entrance lies within the mound.

As soon as a female has hatched, it starts to look for a convenient nesting spot in the immediate vicinity. Olberg (1953) mentions as the origin of what he calls "pseudo colonies" the wasps' preference for the best-situated localities, which are of course limited in number. The female flies and walks about, and tries to dig in every open sandy spot. Sometimes it attempts to take possession of an existing nest or a male's sleeping hole. After a trial period lasting from a few hours to half a day at most, the female starts digging. Sometimes a sleeping hole may be dug for the night only, and is then dug out to a definite nest next day. The total digging period lasts from one to three days (Table 2). When a female takes possession of an existing nest, it also digs, but for a shorter time. When a nest is usurped, the owner is usually chased away (Table 2, CYR and R2). Once an intruder has taken possession of a nest, the original owner hardly ever succeeds in recovering it, although it often keeps wandering about in the neighbourhood a whole day, repeatedly trying to re-enter the nest.

The nests are generally dug rather far apart. When the distance between two nests is less than 10 cm the females tend to fight, seizing each other with their jaws, although this never leads to injury (Fig. 3A, nests 17 and 18). Only once was a female seen bringing a bee to a neighbouring nest.

The tarsae of the first pair of legs are equipped with a row of spines forming a comb with which the sand is moved. When digging, the female usually stands high on the

Table 2. Time needed by a female of *Philanthus triangulum* (F.) to prepare a nest

	wasp no.	start of digging		first bee brought in	
		date	time	date	time
new nest	S6	25/6/68	18.10	28/6/68	16.45
new nest	R9	25/6/68	18.20	28/6/68	14.45
new nest	G15	27/6/68	16.30	29/6/68	13.16
new nest	O19	28/6/68	± 18.00	30/6/68	17.21
new nest	S20	28/6/68	18.49	30/6/68	18.25
new nest	R22	29/6/68	18.04	30/6/68	18.29
new nest	B23	29/6/68	evening	4/7/68	12.25
new nest	O2	18/7/69	18.20	19/7/69	15.13
new nest	S5	1/8/69	9.40	3/8/69	13.41
new nest	O	10/7/70	19.05	11/7/70	18.35
occupation of abandoned nest	B1	23/7/69	10.34	23/7/69	13.05
occupation of abandoned nest	G	15/7/69	9.45	15/7/69	12.26
occupation of abandoned nest	B	3/7/70	16.58	4/7/70	16.27
usurpation	CYR	16/7/69	18.56	17/7/69	18.05
usurpation	R2	25/7/69	18.16	26/7/69	16.25

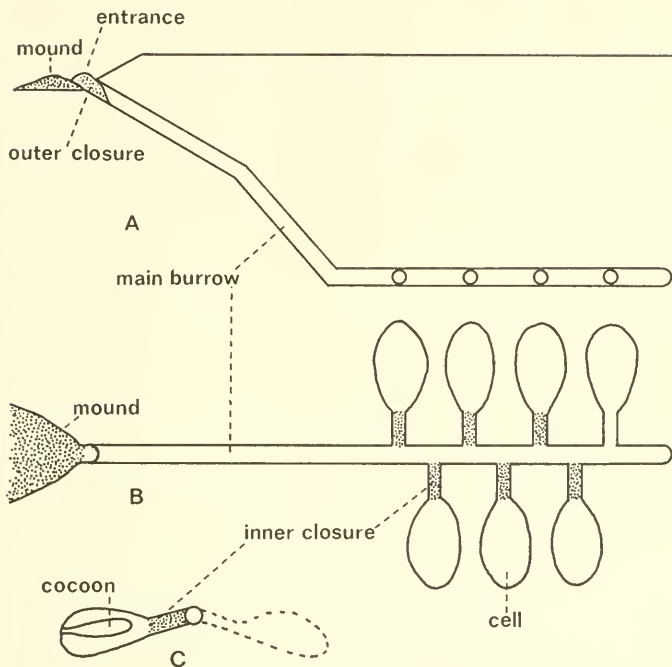


Fig. 4. Generalized nest of *Philanthus triangulum* (F.); A. side view; B. seen from above; C. cross section through horizontal part of main burrow

middle and hind legs and thrusts the sand backwards under the abdomen. Hard obstacles are dislodged with the jaws and dragged away by walking backwards. When this is not possible the insect digs around the obstacle. In removing loose sand the female first walks backwards away from the entrance as far as the edge of the mound and then starts digging furiously while walking forward in the direction of the entrance. The mound obtains its specific form because in walking backwards from the nest, the animal chooses different directions. The outer closure at the entrance is formed of sand pushed by the abdomen from the inside of the nest towards the entrance.

The nest consists of a main burrow running downward with a slope of 30° and varying in length from 15 to 25 cm (Fig. 4). Occasionally, after a short steep descent, the tunnel becomes horizontal. The brood cells lie on both sides of the horizontal segment. When a cell is filled with bees and an egg has been deposited, the cell is closed (inner closure, see Fig. 4). A second horizontal tunnel is sometimes dug from the end of the slanting section, usually about 10 cm deeper in the sand.

In 1969 the total digging activity (in minutes per 15-minute period) was determined

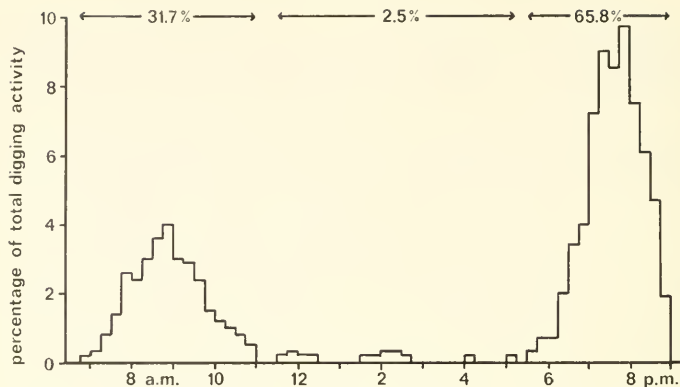


Fig. 5. Digging activity (in minutes) of a number of females in the course of the day, divided into classes of 15 minutes

for a number of females (Fig. 5). By total digging activity is meant: (1) the removal of sand in front of the entrance of the nest, (2) the throwing out of loose sand from inside the nest, and (3) the time spent by the wasp inside the nest apparently busy digging underground (regular expulsion of sand). Fig. 5 shows that the main digging activity occurred between 7 and 11 a.m. (31.7 % of the total) and between 5.30 and 9.00 p.m. (65.8 % of the total). Between noon and 5.15 p.m. only 2.5 % of the digging activity took place. This activity is lower on cold than on hot days and varies between individuals. The abnormally high digging activity shown by the females occupying nests 17 and 18 (Fig. 3A) is explained by the fact that their nests faced each other at a distance of about 6 cm, so that the sand removed by one female continually blocked the entrance to the nest of the other.

c. Foraging.

After awaking and digging, the females fly off. The average duration of this first flight was 31 ± 2 (SD) minutes ($n = 175$). Out of 175 cases the wasp came back in 32 without a bee after the first flight (see e.g. Fig. 2A) and in 143 with a bee (see e.g. Fig. 2B and C). The average duration of later flights was 20 ± 1 (SD) minutes ($n = 269$). These later flights are thus considerably shorter than the first one ($P < 0.005$). Evidently, the females also use the first flight to provide for their own food supply; they are often found on blackberry flowers in search of nectar.

d. Orientation.

When a female flies out, it often performs an orientation flight in the shape of a figure eight with the point of intersection of the loops just over the entrance of the nest. While flying over the nest, the wasp's head is directed towards it. The loops gradually become wider and successively higher. Fig. 6 shows the incidence of the orientation flights (in percent), plotted against the total number of flights for all females. When the number of flights is low, the percentage of orientation flights is about 100. When the number of flights increases, the percentage of orientation flights drops to about 20.

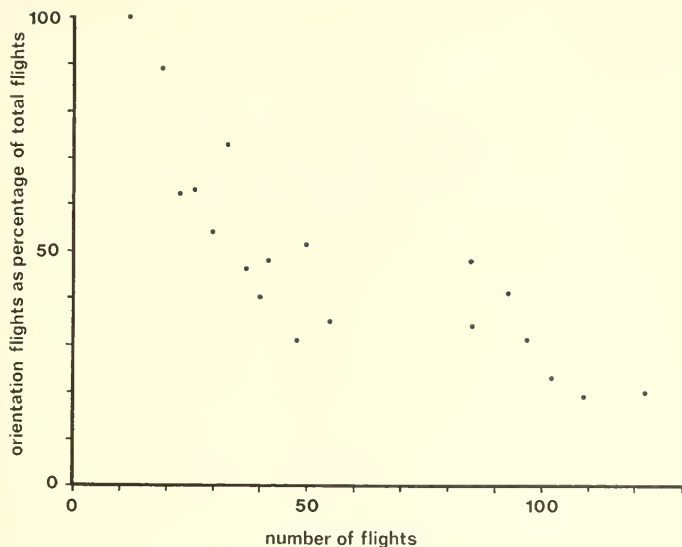


Fig. 6. Percentage of orientation flights plotted against total number of flights, for 19 females

For eight females together a homogeneity test demonstrated that the distribution of the percentage of orientation flights over the day was not homogeneous, $\chi^2 = 48.929$ (21 degrees of freedom), $P < 0.001$ (cf. Table 3). Four females (R, Y, BY, and AG) form a homogeneous group, $\chi^2 = 4.791$ (9 d.f.), $0.75 < P < 0.9$. In this group there is no significant difference between the percentage of orientation flights for the morning

Table 3. Number of flights, with and without orientation flights, made by eight females in the morning and afternoon

wasp no.	morning		afternoon		total no. of flights
	with	without	with	without	
R	4 (29 %)	10	17 (37 %)	29	60
Y	7 (30 %)	16	19 (29 %)	47	89
BY	11 (37 %)	19	25 (41 %)	36	91
AG	6 (27 %)	16	19 (35 %)	36	77
GP	8 (29 %)	20	12 (16 %)	63	103
YW	10 (40 %)	15	13 (15 %)	74	112
RG	5 (45 %)	6	17 (22 %)	61	89
CYR	13 (72 %)	5	23 (37 %)	39	80
	64	107	145	385	701

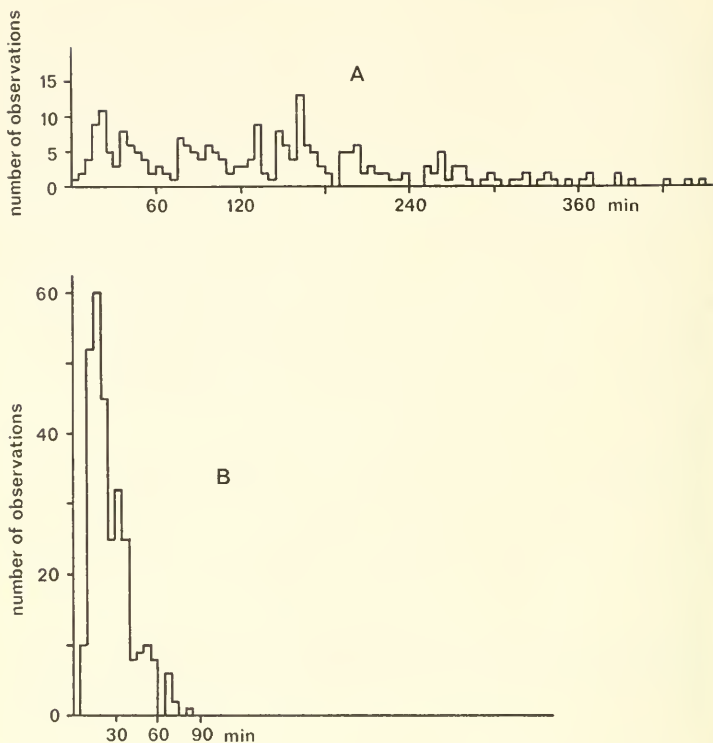


Fig. 7. Intervals between successive homing of *Philanthus triangulum* with prey; A. nest closed; B. nest left open

and the afternoon. The other four females cannot be placed in one group, $\chi^2 = 28.476$ (9 d.f.), $P < 0.005$, though they all showed a higher percentage of orientation flights for the morning than for the afternoon.

The percentage of orientation flights does not seem to be related to the age of the animal or to the heat content of the day in question. In the case of one female that dug a new nest 10 cm from the old one, the percentage of orientation flights did not change.

e. Hunting for bees.

In 1969 the females under study each brought in an average of four bees a day. A female coming home with a bee either immediately closes the entrance behind it (Fig. 2A and B), or leaves it open (Fig. 2C, 2nd and 3rd bee). The time at which bees were brought in was recorded. Fig. 7 shows the duration of the interval between two such

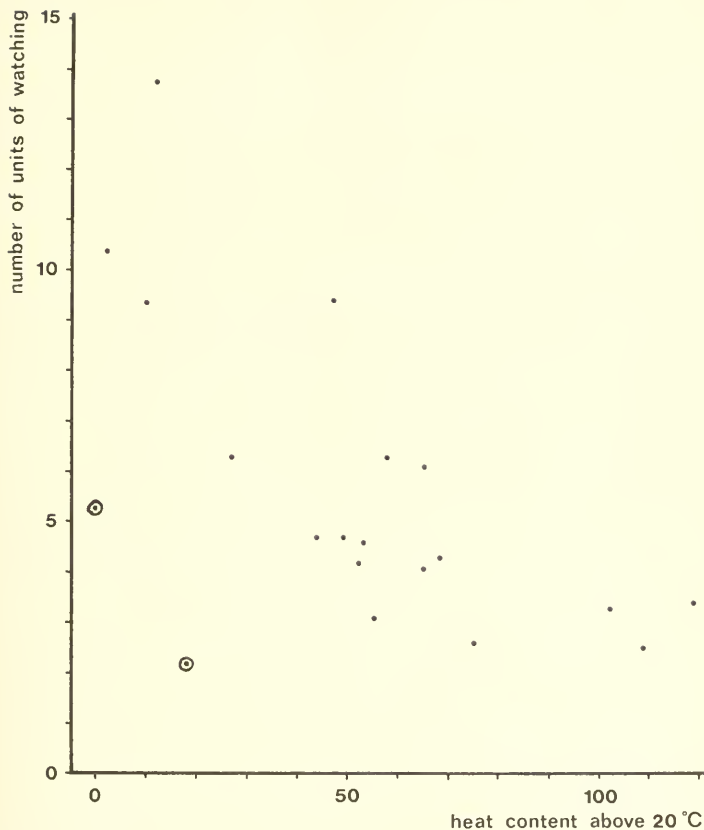


Fig. 8. Number of units "watching" per female per day plotted against heat content above 20°C (encircled points are: one rainy and one cold day)

events. Fig. 7A shows the distribution of the intervals after which the nest was closed, Fig. 7B that for instances when the nest was left open. For closed nests, the average interval is 148 ± 7 (SD) minutes ($n = 243$). For nests left open, the average interval is only 29 ± 1 (SD) minutes ($n = 293$). Fig. 7A also shows that sometimes the female only stays inside briefly, even after closing the nest. This is quite usual for females that have just dug a new nest (Fig. 2A) and possibly also when a female is alarmed while entering. When the female leaves the nest open, a series of 2, 3, or 4 bees is brought in successively at short intervals. Table 4 shows that there is a preference for a series of

Table 4. Distribution of bees captured in series by *Philanthus triangulum* (F.) compared with the theoretical distribution

number of bees captured in one series	actual distribution of captured bees		distribution according to equal chances	
	number of series	number of bees	number of series	number of bees
1	284	284	343	343
2	131	262	142	284
3	104	312	57	171
4	13	52	28	112
		910		910

three bees, and that a single bee is brought in far less often than could be expected on the basis of equal chances. This behaviour creates the impression that the female "plans" to collect a certain number of bees and leaves its nest open while bringing in this series.

In 1970 the average was two bees a day per female, possibly as a result of the cold weather that summer.

f. Closing the nest on leaving.

When leaving the nest, the female rarely closes it. On some occasions, however, it is closed so carefully that the entrance is practically invisible, and on others sand is hastily scratched over the entrance (see e.g. Fig. 2B). During the 1969 observations, seven females never closed their nests, five females did so only in 3 % of the cases, and one female made a closure in 40 % of the cases. In 1970 closing of the nest from the outside was observed only three times. Closure of the nest offers a defence against parasitic flies, but the cuckoo wasp *Hedychrum intermedium* Dahlbom (Chrysididae, Hym.) is able to open closed nests.

g. Dragging out paralysed bees.

Paralysed bees are frequently dragged out of the nest and dumped outside. During the period of observation in 1969 these bees always were entirely fresh, with a full honey stomach. Nineteen females ejected a total of 103 bees, having brought in 1,045 bees in the same period. The removal of bees was observed 73 times. In 72 cases it occurred during the digging period. About one-third of the removed bees proved to have been parasitized by a fly.

h. "Watching".

Especially on cold days the females spend a long time in the entrance. This is called "watching". Fig. 8 shows the frequency of this behaviour per day, plotted against the heat content of the observation days. Each period of watching shorter than five minutes was recorded as one unit. If a period of watching exceeded five minutes, it was divided into periods of five minutes and each such period (eventually together with an additional shorter period) was counted as one separate unit of watching. Fig. 8 shows that watching increases at low temperatures whereas at higher temperatures the value asymptotically approaches 2. The two encircled deviating points coincide with a rainy day and an abnormally cold day, respectively. The average for all the females was 5.6 a day. The daily average per female ranged from 2.1 to 9.8.

In 1970 the impression was gained that watching increased whenever cuckoo wasps (*Hedychrum intermedium*) were present near the nest entrance.

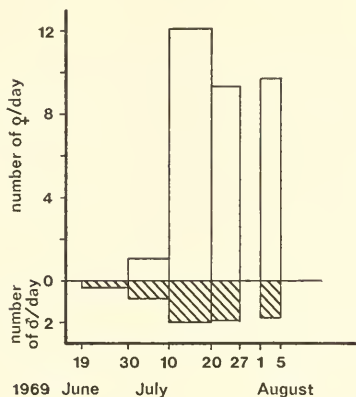


Fig. 9. Numbers of females and males of *Hedychrum intermedium* Dahlbom (Chrysididae, Hym.) collected in the observation area (Naboude, France), in 1969

Life span of the females.

In 1969, the first female was caught on June 25th. On June 26th, one female (R) was marked. This female could be observed continuously. On July 26th and 27th, the activities of this female decreased sharply. Digging activities no longer occurred. On August 1st it flew out twice without bringing in a single bee. On August 2nd this female was found in the heather near the nest. Upon being returned to the nest, it went in quickly and was not seen again. Another female was marked on July 8th, and was still active on August 11th. Thus, the lifespan of these females amounted to at least 37 and 34 days, respectively.

In 1970 two females were marked while they were looking for a place for a new nest, one on July 2nd and the other on the 3rd. On August 12th both were recaptured, at which time they were 41 and 40 days old, respectively.

Second generation.

During the collection performed between 1966 and 1968, it was observed that the population clearly increased in August and that at the time the females looked less worn out and appeared to be larger.

In 1969 a few marked nests, the owners of which were also marked, were kept under observation. On August 2nd a male emerged from one nest and on August 4th an unmarked female from another. On August 11th two unmarked females emerged from a marked nest; a male and an unmarked female from another nest; two unmarked females from a third nest, and one unmarked female from a fourth. The males of the second generation as well as the females are not immediately chased away by the owner of the nest. Once they have flown out, however, they are chased away when they return. On the other hand, a young female looking for a nest occasionally chases away the old owner.

Parasites.

In 1969 there were many cuckoo wasps (*Hedychrum intermedium* Dahlbom, Chrysididae, Hym.) in the vicinity. They usually lie in wait in front of the other species' nests until its owner returns with a bee, to which the cuckoo wasps quickly attempt to attach an egg. They may also open a nest and go inside. Fig. 9 shows the data on captures of cuckoo wasps in the different periods. The male cuckoo wasp appears to hatch earlier than the female, and the numbers of both sexes caught per day show a rapid initial increase and then stay more or less constant. Since captured specimens were killed, captures always concerned new individuals from outside the area of observation.

Observation of marked cuckoo wasps showed that they explore a rather large area and visit nests continually. Marked cuckoo wasps were found at a distance of at least 100 m from the release point. The marked cuckoo wasps were seen near the observed nests several times a day. Apparently, new nests are found accidentally. When a *Philanthus triangulum* comes flying slowly along with a bee, a waiting cuckoo wasp starts walking quickly to and fro in front of the nest and often goes inside for a short time. The *P. triangulum* is alarmed by this, often flying away and sitting on the branch of a pine tree nearby, before attempting to enter the nest again. As long as the cuckoo wasp is there, these attempts may be repeated several times. Finally, the *P. triangulum* quickly enters its nest, followed by one or more cuckoo wasps. Occasionally, it drops the bee and goes inside alone. When a *P. triangulum* wants to dig and sees cuckoo wasps in front of the entrance, it drives them away. A fight may occur, although the intruder is never stung or injured, because it rolls itself up. Cuckoo wasps stay equally frequently near closed and open nests.

In 1970 an average of 2.6 cuckoo wasps kept watch throughout the day near each of the nests under observation. The presence of so many parasites may cause a *P. triangulum* population to die out almost completely in one year's time, as was observed in the Forêt de Campet (Lot-et-Garonne): in 1965, *P. triangulum* was common in this area and there were only a few cuckoo wasps; in 1966, *P. triangulum* was still common in July, but in August showed no numerical increase even though the second generation had hatched. The cuckoo wasps were much more abundant. In 1967, only a few *P. triangulum* were observed and there was a very large number of cuckoo wasps.

Discussion.

In the present paper certain features of the behaviour of the female *Philanthus triangulum* in and around its nest have been described in some detail. The observations concerned awaking, "watching", digging, bee hunting and orientation flights.

According to Tinbergen (1932), *Philanthus triangulum* may sometimes search for as much as ten days for a suitable spot to dig its nest. In southern France this trial period usually lasted half a day to one and a half days, though in cold weather it may take three days. The much longer period reported for The Netherlands may be explained by continuous cold weather. This whole trial period is spent in searching and occasional digging. Although the female does fly off to feed, it never returns with a bee.

Opinions concerning the number of bees deposited per cell vary considerably. Bouwman (1927) found 5 or 6 bees per cell, Tinbergen (1932) mentions 3 to 6, and Fabre (1886) 1 or 2 bees for a male larva and 3, 4, 5, and 6 for a female larva. Vergne (1935), who dug out many cells, always found two bees with a male larva and five bees

with a female larva in a bigger cell. Olberg (1953) mentions 2, 3, or 4 bees for a male larva and 3 to 6, but usually 5, for a female larva.

In our laboratory breeding experiments with *P. triangulum* (Simon Thomas 1966), 614 nests were dug out. The numbers of cells containing from 1 to 6 bees were 11, 254, 135, 60, 41, and 6 respectively (19 %, 41 %, 22 %, 10 %, 7 %, and 1 %). Nests with two bees are therefore the most common. Since all *P. triangulum* had already hatched, it was impossible to determine whether the cells had contained males or females.

Evans (1964) reports that the female of the American *Philanthus lepidus* Cresson buries her bees just inside the entrance and only fills the cells after enough bees have been collected. Similar behaviour is not known for *Philanthus triangulum*. As shown in Table 4, females prefer bringing three bees in succession and as a rule leave the nest open in the meantime. In our laboratory experiments in which, as mentioned above, the cells were mainly filled with two bees, the progeny showed a male-to-female ratio of 5—1. Thus, the supply of three bees in succession does not tally with the number of bees per cell. Conceivably, *Philanthus triangulum* too is in the habit of burying its bees inside the entrance temporarily, in which case it may not use all of them afterwards. This is consistent with the fact that 10 % of the captured bees are dragged out again during the digging period, (page 00), possibly representing the surplus left after the cells have been filled. As already mentioned, the rejected bees are completely fresh, and the honey stomach is often still full. Picard (1903), on the other hand, refers to dead bees he observed outside the nests, but later he says that the females squeeze these bees dry, which means that they were not dead at all but only paralysed.

A remarkable feature is that the females often sit "watching" in the entrance of the nest for very long periods of time. Two possible explanations can be offered for this behaviour. Firstly, this "watching" could be a reaction to disturbance, in this case the observer's presence. Disturbance in the form of cuckoo wasps in front of the nest may also induce "watching". But a more likely explanation seems to be that females are roused to activity by a sufficiently high ground-temperature but that the air-temperature at the entrance turns out to be lower than the ground-temperature. This would cause a conflict situation. We indeed observed that on cold mornings females did open their nest but did not fly away. When the temperature remained low they sometimes sat "watching" for hours.

Philanthus triangulum has very few predators. During the observations, only two females (CG and CW) failed to return to their nests. The two oldest females in our material lived for at least 40 or 41 days. The cause of death could not be verified. Toward the end of the lifespan the wasps' activity declined sharply within a few days, after which they did not emerge from their nests again. This decline in activity showed a strong resemblance to the syndrome caused by parasitism by *Physocephala chrysorrhoea* Mg. (Conopidae, Dipt.). This fly lays its eggs on the abdomen of the adult wasp. The larva bores into the wasp and eats the organs, starting with the least essential parts. We have bred this fly four times from captured *Philanthus triangulum* females.

Beekhuis van Till (1935) found that in The Netherlands *Philanthus triangulum* has two generations a year. Eggs laid in May give rise to adult animals at the end of July. When we were collecting *Philanthus triangulum* in the southwestern part of France, it struck us that there was generally a strong increase of the populations in August and that the females then seemed larger and less worn out by flying. Vergne (1935), who made

observations near Clermont-Ferrand, however, found only one generation a year. Bouvier (1916) mentions having seen several males and females emerging from the same nest in the dunes of Lus-sur-Mer on July 28th, 1901. Only one of these females returned with a bee. Bouvier concluded that *Philanthus* shows a transition to colony formation, but this seems highly unlikely. He probably saw a second generation hatch, especially since he stated that *Philanthus* is solitary before and after this period. According to our observations, a second generation undoubtedly hatches at the end of July or the beginning of August in southern France.

SUMMARY

To investigate conditions for breeding *Philanthus triangulum* (F.) (Sphecidae, Hym.) successfully in the laboratory, an ethological field study was performed in southwestern France. The results provide the following picture.

Each female digs a nest close to the spot where it has hatched. During the period of reproduction, they stay in the same nest. Occasionally, owners are chased away by other females searching for a good spot to dig a nest. The wasps spend the night in their closed nests, and emerge at varying times in the morning. Foraging occurs mainly in the morning during the first flight. Bee hunting (up to 10/♀/day) only occurs when the air temperature is higher than 22° C. Bees are brought to the nest either singly or in series of 2, 3, or 4. While a series is being brought in, the entrance is left open and between two series it is closed. Series of three bees are preferred. The nest is seldom closed when the wasp leaves. When they fly off, the females often perform an orientation flight. The percentage of orientation flights is 100 when very few flights are made, and drops to 20 when there are many flights. Of the bees brought in, 10 % are dragged out again. The females often sit "watching" in the entrance. These periods of "watching" are longer when there are disturbances or during cold weather. The digging inside the nest and pushing out of the sand takes place daily, occurring mainly at the end of the day but also in the morning. The longest stated age of a female in this material was 41 days.

The main parasite is the cuckoo wasp *Hedychrum intermedium* Dahlbom (Chrysididae, Hym.) which is probably able to extinguish a population almost completely in a few seasons. In the southwestern part of France the second generation hatches some time around the beginning of August depending on the summer temperature.

ACKNOWLEDGEMENTS

The authors' warmest thanks are extended to Prof. C. van der Meer, Director of the Pharmacological Laboratory of the University of Amsterdam, not only for his unflagging interest, encouragement, and valuable criticism from the very beginning of the study through the completion of the manuscript, but also for obtaining the funds necessary for repeated research in France.

REFERENCES

- Beekhuis van Till, F. W., 1935, Enige beknopte aantekeningen over het leven van de bijenwolf (*Philanthus triangulum* F.). Maandschrift v. Bijenteelt 38: 258—269.
Beusekom, G. van, 1946, Over de oriëntatie van de bijenwolf (*Philanthus triangulum* Fabr.). Eduard IJdo N.V., Leiden, 162 pp.

- Bouvier, M. E. L., 1916, Quelques observations sur les philanthes. Ann. Institut Pasteur 30: 205—208.
- Bouwman, B. E., 1927, Graafwespen van Nederland. De Levende Natuur 32: 110—116.
- Evans, H. E., 1964, Notes on the nesting behaviour of *Philanthus lepidus* Cresson (Hymenoptera, Sphecidae). Psyche 71: 142—149.
- Fabre, J. H., 1886, Souvenirs Entomologiques IV. p. 191—218. Ch. Delagrave, Paris.
- Hirschfelder, H., 1952, Zur Biologie des Bienenwolfes (*Philanthus triangulum* F.). Zeitschr. f. Bienenf. I: 1—3.
- Olberg, G., 1953, Der Bienenfeind *Philanthus* (Bienenwolf). Die Neue Brehm Bücherei, Akademische Verlagsgesellschaft Geest & Portig K.-G., Leipzig, 85 pp.
- Picard, F., 1903, Note sur l'instinct de philanthe apivore. La Feuille des Jeunes Naturalistes IV, 34e Année, no. 397, p. 17.
- Roth, P., 1917, Notes sur l'instinct et les moeurs du *Philanthus Abdelkader* Lep. St. Fargeau. Bull. Soc. d'Hist. Nat. Afrique du Nord 8: 63—71.
- Simon Thomas, R. T., 1966, A method of breeding *Philanthus triangulum* F. (Sphecidae, Hymenoptera). Entom. Ber. 26: 114—116.
- , 1970, Het individueel merken van *Philanthus triangulum* (F.). Entom. Ber. 30: 149—152.
- Tinbergen, N., 1932, Über die Orientierung von *Philanthus triangulum* Fabr. Z. f. vergl. Physiologie 16: 305—334.
- Vergne, M., 1935, Contribution à l'éthologie et au développement post-embryonnaire de quelques Hyménoptères prédateurs (Sphégiens) en particulier de *Philanthus Triangulum* F. Clermont-Ferrand, Imprimerie Moderne, 141 pp.